THE LIFE HISTORY OF THE SCOLEX POLYMORPHUS OF THE WOODS HOLE REGION

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THIRTEEN FIGURES

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INTRODUCTION

In attempting to determine the life cycle of Crossobothrium laciniatum, a cestode found in the sand shark, (Carcharias littoralis) of the Woods Hole region, attention was at once directed to the cestode larva known as the Scolex polymorphus, which seemed not unlikely to be the young of this species. The studies here described were begun in the hope that these two forms would prove to be a single species, since both are admirable for laboratory purposes and have been so used by students at the Marine Biological Laboratory for many years. It appears, however, that such a relationship does not exist; for the results of the experiments give strong, though perhaps not entirely conclusive, evidence that the Scolex polymorphus develops into the species Phoreiobothrium triloculatum (Linton) and show conclusively that it cannot be the young of Crossobothrium laciniatum. The material was collected and the experiments performed during the summers of 1903 and 1904 at the Marine Biological Laboratory and the United States Fisheries Bureau Laboratory at Woods Hole, Mass., and I am indebted to those in charge of these institutions for substantial aid in the prosecution of the work.

METHODS

The sharks used for infection and the squeteague from which the specimens of the Scolex polymorphus were obtained, were all taken during the summer months in the fish traps near Woods Hole. The sharks were marked by means of numbered copper tags, fastened to the dorsal fin and were kept in wooden fish cars about 5 x 6 x 14 feet, several of which were fastened together to form a float upon which much of the work could be conveniently carried on. At the outset it was necessary to devise some apparatus by which the animals could be held securely in a position convenient for any necessary operation and which could be manipulated with safety by a single person. The holder which was finally constructed consisted of a trough about four and one-half feet in length, formed by nailing two boards together and across their ends two shorter strips after the fashion of a farmer's 'pigtrough.' The top of this trough was covered by a hinged lid which, when fastened down, left the head and tail exposed but held the body of the fish securely along the greater part of its length. The cross piece of one end was hinged to the surface of the float where the holder was being used and to the free end was hinged a support, which, when swung out, held the contrivance at any desired height as the free end was lifted toward the upright position. By working rapidly, it was possible, with the fish thus held securely, to complete the necessary treatment in a few moments, and any more elaborate apparatus providing for the irrigation of the gills seemed unnecessary, since the sharks gave no indication that their vitality had been impaired by this brief exposure to the atmosphere. In operation this holder was safe and in every way satisfactory. The shark was dipped up with

a hand net and placed in the trough ventral side uppermost. Upon fastening its lid, the holder was at once raised to a convenient position and the operator could then quickly introduce any desired object into the mouth cavity. In feeding, the jaws were pried open, a piece of food placed in the mouth and after being guided past the gill arches was thrust down the oesophagus by means of a billet of wood. The oil of male fern and the calomel. used in the attempts to rid the sharks of their previous infection, were given in gelatin capsules having a capacity of 2 cc. These were placed in a piece of galvanized iron pipe, which had been pushed down the oesophagus until it reached the stomach, and the capsule forced down the pipe with a small wooden rammer. This proceeding, or the giving of food, could be accomplished with comparative rapidity and the sharks were often back in the car within two or three minutes after being taken out. There was no sign of the regurgitation of food or drugs, though the bottoms of the cars were carefully inspected during the hours just after treatment, and both food and drugs were found in the digestive tracts of specimens which happened to be examined during the first few days. There can, therefore, be no doubt that both remained in the stomach when once introduced. Further details of methods used are given at the appropriate places throughout the paper.

THE NATURE OF THE SCOLEX POLYMORPHUS

Before describing the experiments in which the larval cestode known as the Scolex polymorphus was used to infect the sand shark, it may be well to offer a word of explanation regarding this form. The name S. polymorphus has been applied by Linton to a cestode larva found in a considerable number of fishes from the Wood Hole region. While most abundant in the squeteague (Cynoscion regalis) and the common flounder (Paralicthys dentatus), he has found it in varying numbers in some twenty-eight other teleosts, the list of which is given on page 413 of his 1901 report. This larva, which I have represented in figs. 1, 2, 3, 4, 12 and 13 of this paper, is frequently met with in a stage slightly younger than the one here shown. In such a young condition it lives in the intestine of its teleost host, moving freely about and attaching itself by means of its four suckers. The slightly older stage which these figures represent and which was used in my experiments, is found in the cystic duct of some of these fishes, notably the squeteague and the common flounder. The specimens which I used for infection purposes all came from the first of these two hosts.

The name Scolex polymorphus originated with Rudolphi ('08) and has since been frequently applied to such larval forms taken from many different fishes, and by Van Beneden ('50) from crabs of the genera Carcinus and Eupagurus. Zschokke ('86), discussing such forms, showed that the mono-, bi- and triloculate types of bothria (figs. 2, 12 and 13 of the present paper), which can be discovered when any considerable number of individuals are examined, are only developmental stages of the same form, and his results indicated that the S. polymorphus with which he worked was the young of the genus Calliobothrium, and not of Onchobothrium as had been previously suggested. These authors of course studied specimens from European waters.

Monticelli ('88) in an extensive paper upon the S. polymorphus of the region about Naples, showed that the larvae, which he found in a large number of fishes, though most common in the flounders, were the young of Calliobothrium filicolle. This conclusion was based upon the close anatomical resemblances between the more advanced larvae and young specimens of C. filicolle and upon experiments in which a species of Torpedo, after being freed of all parasites by starving (a method which his experience and that of the collectors at the Naples station had shown to be effective), was then fed for a time upon specimens of Arnoglossus known to contain the S. polymorphus. As a result of this, young specimens of the C. filicolle were obtained from the torpedoes so treated, and this taken with the anatomical resemblances seemed conclusive evidence. Monticelli has reviewed the literature exhaustively and he gives (p. 89) a list of thirty-six cases in which authors have appended various specific names to the term scolex and made as many different species

of this single form. He refers to these names as synonyms and apparently considers all the forms from whatever host to be the young of a single species.

Although my experiments indicate that the S. polymorphus of the Woods Hole region develops into Phoreiobothrium triloculatum and not into a species of Calliobothrium, a comparison of the larvae, as taken from the fishes about Woods Hole, with the description which Monticelli gives shows that the two types are closely similar, probably almost indistinguishable. The myzorhynchus, bothria with one, two or three loculi, two faint red pigment spots in the neck region of some of the specimens, the general shape of the body and the characteristic movements, are apparently identical. Only in the case of the hosts they inhabit is there any very apparent difference, which is of course necessitated by the differences in the piscine faunas of two such widely separated regions.

In his paper published in 1897, Linton suggested that the S.polymorphus perhaps represents the young of a number of different cestodes, and also that none of the fishes (teleosts) in which he has found it is the true host of either larva or adult. He considers such larvae when found in teleosts to be 'xenosites,' or misplaced parasites, and thinks that the true intermediate hosts may be found among the species of crabs which frequent the feeding grounds of these fishes. In support of this view, he cites the fact that the existence of similar larvae in crustacea has been recorded by Van Beneden ('59). Should this hypothesis prove correct, we should have a case where the transfer from such a host to a teleost fish, while not fatal to the parasite, still presents conditions under which it can develop but a little way beyond the stage already attained. Basing his conclusion largely upon the presence of a median proboscis-like structure (the myzorhynchus) at the anterior end between the bothria, Linton ('97) expressed the opinion that our Scolex polymorphus is the young of the genus Echeneibothrium. This is not, however, as strong a clew as might seem, for in the adult Calliobothrium filicolle, to which Monticelli's larvae developed, this structure is quite degenerate, though well marked in the larva, while in the adult

of Calliobothrium leucartii and Calliobothrium verticillatum there is no trace of such a structure.

In a later paper on the parasites from the fishes of Beaufort, North Carolina, Linton ('04) finds the Scolex polymorphus in many of the fish examined and speaks of the larvae as follows (p. 326):

The larval cestodes, doubtless representing several genera, recorded in Parasites of the Woods Hole Region under the name of Scolex polymorphus, were found in thirty-four of the fifty-nine Beaufort fishes examined. As at Woods Hole these forms are found not only in the alimentary canals of their hosts but also in the cystic ducts of several. They are almost never absent from the cystic duct of Cynoscion regalis. In all cases, where these worms have been obtained from the cystic duct and from the intestine of the same fish, those coming from the cystic duct are larger, plumper, and more opaque than those from the intestine. Some of the older larvae suggest the genera Calliobothrium, Acanthobothrium and Phoreiobothrium.

Again, in speaking of the parasites of the sharp-nosed shark, Scoliodon terrae-novae, under Phoreiobothrium triloculatum, he says (p. 343):

1 scolex, no segments yet developed; length 2 mm.; hooks small. This specimen looks very much like some of the more advanced specimens of Scolex polymorphus which have occasionally been found, save that the bothria have assumed the characteristics of P. triloculatum.

On page 359, under the parasites of the pipe fish, Siphostoma fuscum, he notes that the specimens of the Scolex polymorphus had "bothria with two costae and rudiment at anterior end, suggesting loculi which occur at the anterior end of bothria in Echeneibothrium and Acanthobothrium; no red pigment."

On page 407 under the parasites of the toad fish, Opsanus tau, he speaks of a specimen which was "probably a young Calliobothrium," and of another which "had the characteristic bothria of Echeneibothrium and Rhinebothrium. Its prominent muscular proboscis, (myzorhynchus), if retained in the adult would place it in the former genus." Again, in another lot, "The largest had bothria which resembled those of Calliobothrium and Acanthobothrium, but without hooks." And finally, others which had "red pigment, two costae, one specimen noted with rudimentary hooks (Calliobothrium or Acanthobothrium)" and in another lot a specimen is recorded with the "rudimentary hocks and pigment spots."

Under the parasites of the sole, Symphurus plagusia, there are mentioned specimens which are "comparatively large, with two costae and red pigment like young Acanthobothrium, but without hooks."

Fig. 80, plate 12, shows a young specimen of Calliobothrium with rudimentary hooks, but otherwise much like the Scolex polymorphus.

In view of these later observations of Linton and Monticelli's results, one would expect the Scolex polymorphus from about Woods Hole to develop into one of the species of Calliobothrium found in this region, or perhaps some other species of the family Onchobothriidae, and this last is what I believe happens in the case of the larvae with which my experiments were performed. Since two species of the genus Calliobothrium (C. verticilatum and C. eschrichtii) have been found in our region, by Linton ('99) who records this species from the dogfish (Mustelus canis), and since a considerable number of species belonging to most of the genera of the family Onchobothriidae have been described from Woods Hole by Linton, it would seem not at all unlikely that experiments made by feeding the Scolex polymorphus from the various teleosts to skates, dogfish and sharks might connect these larvae with other genera of the Onchobothriidae. Such experiments would be likely to give precise evidence for or against Linton's belief that the larvae represent the young of more than one form and they might give us data for further consideration of the whole question of xenositism, which Linton suggests is the condition of these larvae when found in teleosts.

In considering the possibility that the various forms of crustacea are the true intermediate hosts in which the development was begun, I have made a careful tabulation of the food of these fishes as recorded mainly by Linton ('99), but also in more detail for a smaller number of fishes in the work of Peck ('95). This

tabulation is not given since it is merely a compilation and the important point ascertained can be briefly stated; namely that crustacea of various sorts, shrimps, amphipods, isopods, crabs, etc., are an important food with almost all these fish. In cases like the squeteague and blue-fish, where they are not so important an item, it is noticeable that various crustacea-eating fish are a common food. This would account for the great numbers of the Scolex in the squeteague, which would then be like a sieve in which were retained many larvae which had come originally from crustacea through the medium of another fish. The flounder, Paralicthys dentatus, is the other fish in which Linton has found the Scolex most abundant. Its food consists of smaller fish and a large proportion of various crustacea, so that in this case the S. polymorphus might be obtained directly from crustacea, or indirectly from another fish. I have also tabulated the food of the fishes from which Linton has *not* recorded the Scolex to see whether crustacea form as large an element in their food supply, but no satisfactory facts can be gathered for the reason that the list of those containing the larva comprises the greater number of our smaller and more common fishes and because, as Linton expressly states, no systematic search has been made and hence the fact that the larvae have not been recorded from any fish may have little importance.

I quite agree with Linton's suggestion that this widely distributed larva, though it does not resolve itself into several easily recognizable types in the larval condition, may eventually be shown to represent the young of more than one cestode, and if I am correct in my conclusion that the S. polymorphus with which my experiments were made develops into Phoreiobothrium triloculatum, whereas the form with which Monticelli worked is the young of Calliobothrium filicolle, this may be the beginning of evidence which will give Linton's interpretation a secure foundation and thus the name 'polymorphus,' which seems originally to have been given because an individual larva of this sort can assume such diversity of shape, may come to have a new significance from the existence of many species under a guise which does not show differences by which each may be recognized. The close resemblance of our S. polymorphus to the forms upon which Monticelli (op. cit.) worked, makes a discussion of the anatomy superfluous beyond what is shown by my figures and their explanations which have been made quite full. The differences are only of a minor nature and hence this author's account is adequate for the anatomy of our forms.

THE NORMAL OCCURRENCE OF PARASITES IN SAND SHARKS TAKEN AT RANDOM

A knowledge of the normal content of parasites found in the sharks, as collected, was important both for its bearing upon the results of treatment which attempted to rid them of all parasites, and upon the results of any artificial infection with young cestodes. There are very few sand sharks examined which have not some infection with Crossobothrium laciniatum, which is the only cestode parasite known to infect the digestive tract of this host in considerable numbers. Some records by Linton ('99, p. 429) are here tabulated as quite representative of any dozen specimens taken at random.

DATE	NUMBER OF SHARKS EXAMINED	NUMBER OF C. LACINIATUM
July 17, 1899	1	20
July 21, 1899		several
August 9, 1899	1	numerous
August 12, 1899	1	2
August 15, 1899	1	1
August 17, 1889		4
August 18, 1899	1	55
August 19, 1899		12
July 20, 1900		47
July 20, 1900		16
August 12, 1900		numerous
August 13, 1900	1	106

Table	from 1	Linton	's record	8
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From my own records, the results are similar, though the counts are usually higher because a careful search was being made for the small young specimens. The following table is from six sharks examined in 1904.

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		C. LACI	NIATUM
DATE	SHARKS	Adult	Young
July 28	1	34	50-
July 30	1	20	10
August 1.	1	30	6
August 3.	1	30	50
August 4.	1	35	25
August 5.	1	50	30

During the years 1899–1910 this parasite has been used for study by the students in one of the courses given at the Marine Biological Laboratory at Woods Hole and we have always been able to obtain an abundant supply when several sharks were available. Sometimes the first shark opened has yielded all the material needed and it has never been necessary to examine more than four or five. Most of the actual counts recorded in my notes in 1903–04 were made upon sharks in which search was being made for specimens showing the early stages of proglottid formation and for this reason the sharks recorded are perhaps those which seemed, when first opened, to have an abundance of the parasites. Linton's records as given in the first table are therefore more fairly representative.

As a further example of their abundance, my notes record the examination on August 11, 1904, of ten sand sharks, taken in the traps on that date. Every one of the ten was infected and in only two cases was the number of the parasites noticeably small. Count was not made because it was evident that the amount of infection averaged substantially the same as that shown by Linton's record.

From these data it is evident that one rarely finds a sand shark which has not some infection; and from the fact that the worms may be found in all stages of development, from the specimens just beginning to form segments to the large adults which are shedding motile proglottids, one may conclude that the source of the infection has been in contact with the sharks within a quite recent period, if, indeed, it is not acting upon them throughout the summer.

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THE INFECTION OF SAND SHARKS WITH THE SCOLEX POLYMORPHUS

The first attempt at infection of the sand sharks with the Scolex polymorphus was made with fish which had been held without food for a period of three weeks, a treatment which Monticelli ('88) found effective in ridding a species of Torpedo of its Calliobothrium. In all, eleven fish were so treated and each was then given all the larvae obtainable from twelve squeteague, a dose which was estimated at not less than five hundred larvae for each shark. Each fish was fed at the time of the infection and in the three weeks after infection, during which they remained alive, each was fed four times. For food, the flesh of the squeteague was used. an amount about equal to one-third, or one-half the bulk of a good sized fish being used at a feeding; my guide in this matter being the size of the pieces of food commonly found in the stomachs of recently captured sharks, which had fed under natural conditions. Judging from the rate of digestion, as observed on several occasions, this amount of food was unnecessarily large. Such an amount once a week would be ample for sharks in captivity. Moreover, the choice of food was not good; for one may be introducing almost any kind of a cestode larva by feeding the flesh of a teleost fish. In using for infection sharks which had not received any treatment, other than the three weeks' starving above mentioned, I was, of course, aware that one might expect each one of them to contain the normal infection of C. laciniatum. It seemed, however, that if the S. polymorphus from the squeteague did represent the larval form of Crossobothrium, it would develop readily in its normal host, and that the introduction of a very large amount of infection would perhaps give the fish thus treated so many young worms all the same size, as to show that they could only have come from the larvae introduced by the experimental infection.

Three weeks after the infection these eleven sharks were killed and their digestive tracts carefully examined. Each contained adult specimens of C. laciniatum in numbers sufficient to indicate that all the sharks had their normal complement of parasites and therefore that the three weeks without food had produced no effect. In eight of the fish there were a considerable number of young specimens of C. laciniatum in all stages of proglottid formation, but as similar stages are commonly found in all sharks (Curtis, '03 and '06), their occurrence here was no evidence that they had come from the introduced Scolex polymorphus, and the diversity of their stages made any such interpretation out of the question. In these eight specimens there were found in addition to the young and adult C. laciniatum, an unusual number of individuals of the species Crossobothrium angustum, which Linton ('99) p. 426), records as a frequent parasite of the dusky shark, Carcharinus obscurus, and the blue shark, C. milberti. Although present in greater numbers than I have found in any other lot of sand sharks, these C. angustum were of all stages from young to adult and there seemed, therefore, no evidence which would connect them with the larvae which had been introduced by my infection. In the whole number of sharks I found upwards of fifty young of another cestode, all in about the same stage, and with well developed scolices and the segmentation into proglottids just beginning. Because of their conspicuous and characteristic bothria, these were at once recognizable as the young of the species Phoreibothrium triloculatum, a form which Linton has described from the dusky shark and which is represented in figs. 5, 6, 9, 10 and 11 of this paper. Unfortunately, my records give only the fact that each of these sharks contained some Phoreiobothria and fail to give their distribution in the individual sharks.

The occurrence of this species in the sharks of this experiment would indicate, when taken alone, hardly more than that P. triloculatum is sometimes found in the sand shark, even though the only sand sharks in which I have found it are the ones previously infected with the Scolex polymorphus. The fact that the individuals were all of about the same early stage is more important, though not much stress can be laid upon it because of the failure of my records to state the distribution of these worms in the individual fish. I regard the results of this attempt at infection, which was the only one I was able to carry through in the first summer of my work, as valuable only because they support the more satisfactory results obtained in the work of the following summer. A further discussion is, therefore, deferred until the results of the later work have been presented.

Having been unsuccessful in the attempt to reduce the number of parasites by the process of starving, for as long a time as was available, if the sharks were to be used for any subsequent experiments, attention was directed at the beginning of my second summer's work to the discovery of an effective method by which the sharks could be entirely freed of their cestode parasites. For this, I used the oil of male fern, one of the most powerful vermifuges used in human and veterinary practice. Following this practice, the dose of the oil was followed after an interval of from twenty-four to forty-eight hours by one of calomel. The manner of introducing these drugs into the stomach of a shark is explained in the earlier section of this paper where the general methods of work are given. In the tables upon the pages which follow will be found the detailed results obtained with the several lots of sharks treated in this manner. The necessary general explanations will be given in the discussion of the first table, while in the discussion of the subsequent tables I shall give only the facts which the tables show.

TABLE 1

5 sharks, captured before July 2, kept without food until July 22

DATE	NO. GIVEN SHARK IN THIS SERIES	CONDITION OF SHARK AT DEATH	CESTODES IN SPIRAL VALVE	REMARKS
July 23	No. 1	Dying	6 C. lacinia- tum found dead	
July 26	Nos. 2, 3, 4, and 5	Killed	No signs of cestodes	Mucous mem- normal

July 22, all sharks given 2 cc. each of oil of male fern July 23 the four surviving sharks given 1 cc. of calomel

Table 1 shows the results obtained with five sharks which were starved from three to four weeks after capture and then given

2 cc. of oil of male fern, followed twenty-four hours later by about 1 cc. (measured dry) of calomel. The dates and other points of importance are shown in the several columns, under appropriate headings. For convenience of reference, each shark is given a number. The column which shows the 'condition at death' is inserted because specimens did not always survive the treatment and thus some of those examined had died from its effects. Such specimens are marked 'dead' while others which were killed because they seemed about to die are marked 'dving.' The specimens which are marked 'killed' are those which appeared to be in perfect condition when they were taken and killed for examination. The specimens found soon after death ('dead') and those which were killed when they seemed likely to die ('dying'), presented data of some value, for the reason that under normal conditions the death of the shark is not followed at once by the death and consequent disintegration of the parasites. One finds that living cestodes can be obtained from untreated sharks, which have been dead in the water, or lying exposed to the air upon the wharf for five or six hours and I have often seen, in my work with the students at the Marine Biological Laboratory, spiral valves left exposed to the air all day yielding an abundance of C. laciniatum which were still alive and seemingly about as active as if taken from a shark just killed, and these worms if put into sea water may live for as long a period as fortyeight hours. In no case of an untreated shark which, on being injured by rough handling in my cars or by the collectors when first captured, was killed before it died from the effects of this handling did I find the approach of death in the host killing the parasites. We may therefore conclude that when, in a shark which has died very recently, or in one which has been killed because death seems approaching, there are found dead Cestodes, the worms have been killed by the drugs and not by the actual, or approaching, death of the host. Such cases have for this reason a sufficient value to be considered in the series. The objections against them are, first, that they do not represent individuals taken at random, and second, that it is of no value to show that the worms are killed in the sharks which do not survive the treatment while other worms are not killed in the sharks which do survive. It should be remembered, however, that such non-survivors do not represent the weakest individuals in any lot, for the strongest were probably the ones which fought hardest when put in the holder and such very active sharks received rougher handling and perhaps they sometimes died from this cause. With these reservations, the specimens found soon after death and those killed when about to die, may be cited as showing the immediate effect of the drug upon the parasites.

An important point, noted in some of the tables, is that about twenty-four hours after the dose of oil, that is, when the calomel was given, numbers of dead Crossobothria were squeezed from the anus as a shark was placed in the holder. Many entire worms of all sizes were thus obtained and these when placed in sea water slowly disintegrated, showing no signs of life, as they might have done if only stupefied by the oil.

Of the five sharks here recorded, No. 1 was not in good condition, though death did not seem near at hand, when it was killed the day after the oil was administered. It contained only dead C. laciniatum. Three days after the calomel was given the four remaining specimens were killed and examined, with the results which are shown in the table. They were all in good condition and the mucous membrane seemed quite normal. I may here state that my examinations of the spiral valves throughout this work have been most careful. In each case the outer wall was split longitudinally along one side and the cut continued down across the spiral folds to the opposite side. A similar cut was made across each fold along the middle of each half of the valve and the inner surface thus exposed as four parallel rows of triangular flaps, which were then examined one at a time under a lens. Where there was any such amount of chyme as to obscure the surface of the mucous membrane the valve was washed until clean and the washings examined in shallow dishes against a dark background.

Table 2 shows the results in five sharks, which were given a heavier dose of the oil of male fern, and the calomel after an interval of forty-eight hours. After the dose of oil, shark No. 1

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TABLE 2

5 sharks, captured before July 1, kept without food 3 to 4 weeks

July 18, all sharks given 4 cc. each of oil of male fern July 20, the three surviving sharks given 1 cc. each of calomel

DATE	NO. GIVEN SHARK IN THIS SERIES	CONDITION OF SHARK AT DEATH	CESTODES IN SPIRAL VALVE	REMARKS
July 19	No. 1	Dying	1 strobilla dead	Traces of oil in stomach
July 20	No. 2	Dead	No signs of cestodes	Digestive tract considerably decomposed
July 21	Nos. 3, 4 and 5	Killed	No signs of cestodes	Mucous mem- brane in good condition

TABLE 2a

1 shark, captured about June 15, and kept without food

July 1, given several cc. of oil of male fern diluted with ether.

DATE	NO. GIVEN SHARK IN THIS SERIES	CONDITION OF SHARK AT DEATH	CESTODES IN SPIRAL VALVE	REMARKS
July 5		Killed	No signs of	f cestodes

seemed to be dying and was killed with the results indicated. No. 2 was found dead, but was a good deal decomposed and so the absence of worms may not mean much. The three surviving specimens, which were killed twenty-four hours after the calomel, were without any cestodes.

The results of these two experiments may be criticised on the ground that the sharks were not left alive long enough to show that more would not have died from the treatment, but my experience has shown that when the animals survived this treatment for two or three days the subsequent mortality was not likely to be greater than among any other sharks kept in confinement. Some of the sharks noted in other tables were kept alive a much longer time.

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Before I began using the gelatin capsules a single shark which had been in captivity a few days was given some oil of male fern diluted with ether. How much actually got into the stomach I do not know, as some was spilled in pouring the mixture down the tube which was thrust into the oesophagus. No calomel was given. Five days later when the specimen was examined there were small traces of the oil still in the intestine and no worms were found.

TABLE 3

20 sharks, captured July 4 to 7, kept without food

DATE	NO. GIVEN SHARK	CONDITION OF	CESTODES IN	REMARKS
DATE	IN THIS SERIES	SHARK AT DEATH	SPIRAL VALVE	REMARKS

July 25, all sharks given 2 cc. each of oil of male fern

July 26	No. 1	Dead	9 scolices and bits of strobi- læ, all dead	not noticeable
July 26	No. 2	Dying	2 dead	Size of worms not recorded
July 26	No. 3	Dying	20 dead and in the faeces	Size of worms not recorded
July 26	No. 4	Dead	4 dead and in faeces	Decomposition of intestine not noticeable

July 26, the sixteen surviving sharks given 1 cc. each of calomel

July 27	No. 5	Dead	No worms	Decomposition just begun
July 28 July 28	No. 6 No. 7	Dead Dying	No worms No worms	Mucous mem- brane normal
July 31	No. 8	Killed	No worms	Mucous mem- brane normal

August 2, the twelve surviving sharks each fed on shark's flesh

August 7	No. 9	Dead	No data	Considerably
				decomposed

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TABLE 3-(Continued)

August 28 No. 10 Killed No worms August 28 No. 11 Killed No worms August 28 No. 12 Killed 1 Crossobothrium laciniatum August 28 No. 13 Killed 1 Crossobothrium laciniatum August 28 No. 13 Killed 2 Crossobothrium laciniatum August 28 No. 14 Killed 1 Crossobothrium laciniatum 2 Crossobothrium laciniatum young 2 Crossobothrium laciniatum 3 Crossobothrium laciniatum scolices 1 Crossobothrium laciniatum	DATE	NO. GIVEN SHARK IN THIS SERIES	CONDITION OF SHARK AT DEATH	CESTODES IN SPIRAL VALVE	REMARKS
	August 28 August 28 August 28	No. 11 No. 12 No. 13	Killed Killed Killed	No worms 1 Crossobothriu 1 Crossobothriu 2 Crossobothriu young 2 Crossobothriu scolices	um laciniatum um laciniatum um laciniatum

August 15, the eleven surviving sharks each fed on shark's flesh

The six remaining sharks survived the treatment to this date and later, and were used for infection experiments. When examined they gave results as follows:

August 11	No. 15	Dead	No worms	Badly decom-
	1			posed
August 22	No. 16	Dead	No data	Badly decom- posed
August 29	No. 17	Killed	No worms	Normal
August 31	No. 18	Killed	1 Crossobothri	
August 31	No. 19	Killed	medium siz 8 C. laciniatur	e n large, scolices
			5 C. laciniatur	n, small
August 31	No. 20	Killed		n, medium size
			10 C. laciniatur	n, sman

Table 3 shows less satisfactory results than the foregoing, the net results being as follows: without parasites 11, found dead and so decomposed that no data were obtained 3; still infected 6.

If the survivors alone are considered the results are not nearly so good, for out of ten surviving specimens (Nos. 8, 10, 11, 12, 13, 14, 17, 18, 19, and 20) we have only four (Nos. 8, 10, 11, and 17) which are entirely free of cestodes, while there are six (Nos. 12, 13, 14, 18, 19, and 20) which are still infected. Of these six, Nos. 12, 13 and 18 have but a single parasite, so the chances are that some parasites have been eliminated, but Nos. 14, 19 and 20 show so many that one could not fairly claim any reduction as a result of the treatment. When, however, those specimens which were killed when they seemed in bad condition are taken into account, it is evident that many worms must have been eliminated, and the results indicate the elimination of many of the parasites from this lot of sharks, probably of all of them in those sharks which died from the treatment, but they also indicate that the dose as here given cannot be relied upon.

TABLE 4

12 sharks, captured before July 2, kept without food

DATE	NO. GIVE: IN THIS			NDITION OF RK AT DEATH	CESTODES IN SPIRAL VALVE	REMARKS			
July 28, each shark given 2 cc. oil of male fern July 29, each shark given $\frac{1}{2}$ cc. calomel									
August 30	No.	1		Dying	No worms	Traces of oil and calomel in gut			
August 1	No.	2		Killed	No worms	Gut normal			
August 3	No.	3		Killed	No worms	Gut normal			
August 4	No.	4		Killed	No worms	Gut normal			
August 16	No.	5		Dead	No data	Decomposed			
August 11	No.	6		Killed	1 C. laciniatur	n, scolex			
August 11	No.	7		Killed	3 C. angustum	, small			
					3 C. laciniatur	n, small			

August 18, the five surviving sharks each fed on shark's flesh

August 28	No. 8	Dead	No data	Decomposed	
August 29	No. 9	Killed	1 C. laciniatun	a, small	
August 30	No. 10	Killed	2 C. laciniatum small found		
			at very ant	erior end of	
			spiral valve		
August 30	No. 11	Killed	No worms		
August 30.	No. 12	Killed	2 C. laciniatur	n, large and	
			with ripe p	roglottids	
			1 C. laciniatur	n, small	

Table 4 shows five cases of entirely successful expurgation (Nos.1,2,3,4 and 11). Specimens Nos.9 and 10 had respectively one and two worms, while No. 12, since it has two large worms with ripe proglottids, does not justify the conclusion that the number of the parasites was even reduced, and No. 7 must be regarded in the same way.

TABLE 5

DATE	NO. GIVEN SHARK IN THIS SERIES	CONDITION OF SHARK AT DEATH	CESTODES IN SPIRAL VALVE	REMARKS
Augu	st 17, all sharks	given 2 cc. eac	h of oil of male	fern
August 18	No. 1	Dying	No worms	Dead worms from anus in handling
August 18	No. 2	Dying	• No worms	1
August 18	No. 3	Dead	No worms	Dead worms from anus in handling

12 sharks, captured July 25 to August 6, kept without food

August 18, the nine survivors given ¹/₄ cc. each of calomel

August 30	No. 4	Dying	No worms	Gut normal
August 31	No. 5	Killed	No worms	Gut normal
August 31	No. 6	Killed	No worms	Gut normal
August 31	No. 7	Killed	No worms	Gut normal
August 31	No. 8	Killed	No worms	Gut normal
August 31	No. 9	Killed	No worms	Gut normal
August 31	No. 10	Active	No data	Escaped
August 31	No. 11	Killed	8 C. laciniatum,	medium size
August 31	No. 12	Killed	4 C. laciniatum,	medium size

Table 5 has twelve sharks, less one which escaped during the handling. Of these eleven individuals, Nos. 5, 6, 7, 8 and 9 were without any infection, Nos. 1, 2, 3 and 4 did not survive, but showed that the drug had killed the parasites. Nos. 11 and 12 have respectively eight and four specimens of C. laciniatum and hence must be counted as against the effectiveness of the treatment.

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It so happened that no shark, in which the Crossobothria survived, was killed among the first in any lot; as may be seen by reference to the dates on tables 1, 2, 3, 4 and 5. Thus by the 11th of August my records showed thirteen sharks which were killed when in perfectly good condition, six others which were killed, when it seemed that they were likely to die, and seven others, which died from the treatment and in not one of these had I found a single living Crossobothrium. This seemed to demonstrate the effectiveness of the single treatment with the oil of male fern, which was therefore continued, the sharks which survived it being kept for infection with the S. polymorphus. Later, when sharks began to appear in which some of the worms had survived, the season was so far advanced that there was neither

TABLE 6

9 sharks, captured August 6 to 9, kept without food

DATE	NO. GIVEN SHARK IN THIS SERIES	CONDITION OF SHARK AT DEATH	CESTODES IN SPIRAL VALVE	REMARKS
	ust 18, all sharks August 19, all dead Crossoboth	sharks given ½	cc. of calomel	
ugust 30	No. 1	Dead	No worms	Decomposed
August 30	. No. 2	Alive	No data	a little Escaped

August 30, gave the seven survivors 3 cc. each of oil of male fern

September 1	No. 3	Dead	NO WOIMS	No noticeable decomposi-
September 1	No. 4	Dead	No worms	tion No noticeable decomposi- tion
September 2 September 2 Ssptember 2 September 2 September 2	No. 7 No. 8	Killed Killed Killed Killed Killed	No worms No worms No worms No worms No worms	Gut normal Gut normal Gut normal Gut normal Gut normal

TABLE 7 .

DATE OF SHARK'S CAPIURE	NO. GIVEN IN THIS SERIES	DATE OF TREATMENT WITH O.M.F.	FED	INFECTUD	FED	REMARKS
July 6 July 6 July 6 July 15 July 6 July 6 July 1 July 1	No. 2 No. 3 No. 4 No. 5 No. 6 No. 7 No. 8	July 25 August 1-3 August 1-3 August 1-3 August 1-3 August 1-3 August 1-3 August 1-3	August 4 August 10 August 10 August 10	August 9 August 8 August 8 August 11 August 10 August 9 August 9 August 11 August 11	August 10 August 10 August 10 August 10 August 10	Fed at time of infection

Showing the results of infection experiments

TABLE 7—Continued

Showing the results as in tables 1 to 6

DATE	NO. GIVEN SHARK IN THIS SERIES AS ABOVE	CONDITION OF SHARK AT DEATH	CESTODES IN SPIRAL VALVE. REMARKS
August 12	No. 1	Dead	Many S. polymorphus found attached to the wall of the stomach and to the bit of the squeteague's stomach in which they were placed when intro- duced. The gut was slightly decom-
	NT O	DI	posed, but the larvae were still alive.
August 16		Dead	No data. Badly decomposed
August 31	No. 3	Killed	Many small Phoreiobothrium trilocu- latum. See text p. 846
September 1	No. 4	Killed	3 C. angustum, small
		1	3 C. laciniatum, small
	1		7 Phoreiobothrium triloculatum.
September 1	No. 5	Killed	3 C. laciniatum, small.
September 1		Killed	8 C. lacininatum, large with the long
	1 1101 0		neck region
			5 C. laciniatum, small
September 1.	No. 7	Killed	10 C. laciniatum, small.
September 1.	10.7	inica	7 C. laciniatum, medium
September 2.	No. 8	Killed	3 C. angustum, small
Beptember 2.	110.0	Isilieu	Many Phoreiobothrium triloculatum
Contombon 9	No. 9	Killed	1 C. laciniatum, scolex only.
September 2.	110, 9	Innea	Many Phoreiobothrium triloculatum
			Many Phoreiobothflum triloculatum

the time nor the material for trying a modification of the treatment upon any considerable number of sharks. Only nine sharks were differently experimented upon and the results obtained are represented in table 6, the net results of which are; without infection, 5; found dead but in sufficiently good condition to give reliable evidence that the worms had been killed by the drug, 3; escaped, 1.

The results of all the expurgation experiments may be summarized in the table which follows:

TABLE 8

Showing net results from all experiments in treatment with oil of male fern

TABLE REFERRED TO	SURVIVIN	G SHARKS	SHARKS WHICH DIED UNDER THE TREATMENT, BUT IN WHICH THE WORMS WERE ABBENT OR HAD BEEN KILLED BY THE OIL OF MALE FERN			
	No infection	Still infected	Killed when seeming likely to die	Found dead	Total	
1	4		1	1	5	
2	3		1	1	5	
3	4	6	3	4	17	
4	5	4	1		10	
5	5	2	4		11	
6	5		3		8	
	26	12	13	5	56	

In this table, a few specimens which were found dead and so decomposed as not to yield reliable data are omitted. The specimens which survived treatment are of course most important and stand in the proportion of 26 for and 12 against the success of the attempted expurgation. Of the non-surviving sharks we have 13 specimens taken while still alive and all showing that worms were killed, as a result of the treatment and some time prior to the death of the shark. When one compares the number of worms found in these treated sharks with the tables and records showing their prevalence in sharks which have had no such treatment, it will be quite evident that a large proportion of the parasites must have been eliminated even by the single dose.

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In those sharks which were given the double dose of o. m. f. (table 6) not a single cestode was discovered, but as only eight specimens were thus treated the number of trials is insufficient to show that even this treatment may be regarded as always effective. It is perhaps too much to expect a treatment that will be entirely effective in every instance, nor is such a treatment necessary, for a stray worm or two in one shark out of a dozen would still give us a result good enough for practical working purposes. Unsatisfactory though my results are, they do, I think, justify the belief that a little more experimenting along the line of repeating the dose one or more times would develop a method of treatment sufficiently effective for working purposes, i.e., will eliminate all the parasites, except in rare instances, without killing too many of the sharks. If such a method can be found, the sharks thus expurgated could be used in a variety of experiments. For example, by introducing young Crossobothria into a shark one might expect to find out more than we now know about the rate of growth and the maturing of proglottids in the cestoda, and another point worth examining would be the truth of the current idea that it is the inability of the cestode to survive in the wrong host which limits the habitat of a given species of parasite to a single host, or to a few closely related hosts. This latter point might, indeed, be investigated by the infection of sand sharks with larval forms other than the ones known to occur in that host, but where the normal infection is so great the examination of the specimens would be much easier if the host was first freed of all infection.

An insufficient supply of squeteague during the latter part of the second season made it impossible for me to make more than a few infections after the method of treatment, as above described, had been established. Only nine sharks were so infected and none of these was killed until about three weeks after the infection had been introduced. Hence the material is wanting to show my transitional stages between the S. polymorphus and the young specimens of Phoreiobothrium (figs. 9, 10 and 11) which I believe to have come from this larva. This lack of early stages resulted not because I chose, having only a limited number of infections, to let them all run as long as possible, but because the sharks first infected were kept to run longest; while later infections were planned for the earlier stages, an arrangement which would give the most extensive time results in a limited time. When, however, the time came for infecting the sharks from which to secure the earlier stages, the squeteague could not be obtained in numbers sufficient to yield the larvae for infection purposes.

Of the nine specimens, two died in the cars and from one of these two no data were obtained, so there are only seven specimens from which entirely reliable conclusions can be drawn. The sharks used were all starved for three or four weeks after their capture and then given 2 cc. each of the oil, followed twentyfour hours later by about 0.5cc. of calomel. They were all specimens which had survived this treatment and the history of each individual previous to the time of the infection is given in the first half of table 7. Since there is no evidence connecting the genus Crossobothrium with the S. polymorphus, this table may also be used to furnish data on the success of the attempt at expurgation. The first part of the table gives the dates of capture and of the treatment with the drugs, between which events the sharks were kept in the cars without food. The dates at which they were fed are also shown for comparison with the dates of infection. Each shark is numbered, as in the previous tables, and these numbers are repeated in the second half of this table where the results of the examinations for parasites are tabulated in a manner similar to that followed in the tables for treatment with the oil.

In introducing the S. polymorphus into these sharks I took the portion of the cystic duct containing the larvae from twelve squeteague, and placed these in the little sac obtained by cutting off the end of a squeteague's stomach. This sac was turned wrong side out to avoid any possible injury from direct contact with the mucous membrane of the squeteague. The infection thus prepared was introduced into the shark's stomach by pushing it through a piece of iron pipe having a diameter sufficient to admit such an object without undue pressure. For food, I used the flesh of another sand shark in preference to that of a teleost, since there is the minimum likelihood of finding any cestode larvae in the flesh of a large shark; whereas a teleost may, in addition to its normal parasites, contain almost any thing in the way of a 'xenositic' larva. All the sharks were fed shortly before or after their infection, as is shown in the first half of the table.

The latter part of table 7 shows the results when these same sharks were examined for parasites, and by reference to the number given each specimen, one may follow any one fish through the two parts of the table. The only shark examined soon after the infection is No. 1, which was found dead. In this shark, specimens of the S. polymorphus were found adhering to the surface of the shark's stomach and to the remains of the bit of squeteague's stomach in which they had been introduced. Although this specimen was not found until decomposition was quite in evidence, these larvae still showed some slight movements and had therefore survived in the stomach for a period of three days. Shark No. 2 died during my absence from Woods Hole and was so badly decomposed when found that no data were obtained. In the spiral valve of specimen No. 3 there were a very large number of young Phoreiobothrium triloculatum (figs. 9, 10 and 11). I collected and preserved some thirty-five of these worms, but this number represents only a small part of those present. Owing to their minuteness when only the delicate posterior end can be seen protruding from between the villi of the intestine and the tenacity with which their powerful hooks enable them to retain their hold, these larvae are often very difficult to detach from the walls of the spiral valve, though they may be large enough to be easily recognized. There must have been present in the shark many more than I collected; for taking into account the ones actually seen but not collected, I estimated at the time that there were a good many more than one hundred of these young worms in this single fish. A fact of perhaps more importance than their numbers is that in any one shark they were all in the same stage of development.

Shark No. 4 shows three specimens of C. laciniatum which are to be regarded as worms which survived the expurgation treatment. Seven small specimens of P. triloculatum were collected, but in this case it was evident that the valve contained a much smaller number of these than the previous one. My notes taken at the time state that no more were seen in addition to those actually collected, although there may have been some toward the anterior end where the villi are longest. Specimens Nos. 5, 6 and 7 all present evidence against the effectiveness of the vermifuge. In 6 and 7 the numbers of surviving cestodes is so great that no certain effect from the drug is indicated. There is perhaps some significance in the fact that here, as in some other cases where the worms are found surviving the effects of the oil, the proportion of young to adult specimens is somewhat increased. This may indicate that the drug is more effective with the large worms which have long bodies extending among the folds of the valve than with very young ones which may often be almost buried among the villi and so escape the full effects of the drug. In this table there are recorded from specimens 4, 5, 6, 7, 8 and 9 a total of 43 surviving Crossobothria. Of these only 9 are beyond the period of segmentation into proglottids and from what we know of the proportions in which the young and old are commonly found it would seem that the drug has destroyed more adult than young worms. This conclusion is of course based upon my belief that these young Crossobothria have not come from the introduced S. polymorphus.

In sharks Nos. 8 and 9 the same condition was found as in No. 3, namely, so many specimens of small P. triloculatum that the counting them was an impossible task. Later when I examined very carefully the preserved specimens I found that the Phoreiobothria from any one shark were of uniform size, but that when those from different sharks were compared there was some difference in the size attained. For instance those from specimen 9 are almost twice the size of the ones from specimen 3. This difference in size is noticeable only in the body portion of the larvae, the scolices being of very uniform size.

The presence of the C. laciniatum and a few C. angustum, although there are more young specimens among them than one would expect to find in sharks taken at random, does not seem to indicate anything except the ineffectiveness of the attempt at expurgation. There can be no interpretation of the facts which would show that the S. polymorphus had given rise to these Crossobothria.

Despite the lack of intervening stages between the S. polymorphus and the specimens of P. triloculatum, which I found in these sharks, I think there is some pretty good evidence that the latter have developed from the introduced S. polymorphus. First, the examination by myself, and also by Linton, of a large number of sand sharks at various times has never shown that young or adult specimens of Phoreiobothrium triloculatum are to be found as regular parasites of this shark, or as frequent 'xenosites.' I have never found this form in any sharks except those which I infected with the S. polymorphus. It is very probable, however, that one might at any time find stray specimens of this worm, since the squeteague is a not uncommon food of this shark. The failure to find it in any of the sharks I have examined would indicate that it does not often survive, when introduced in nature along with the squeteague, and in my experiment only a small proportion of the larvae introduced have survived. Second, the specimens of P. triloculatum which I found in any one shark were of very uniform size, and unless we suppose that there is some limit to their growth, when in an abnormal environment (the wrong host), this would indicate that they all entered the shark at about the same time. In the third place this conclusion is also in line with the results of Monticelli ('88) who has shown that the S. polymorphus of European waters develops into the genus Calliobothrium, which belongs to the same family as Phoreiobothrium, a fact which is further discussed in the portion of this paper which deals with the nature of the S. polymorphus.

Attention should here be directed to one point which has perhaps suggested itself from the examination of the figs. 7-13. This is that the specimens of the young P. triloculatum (figs. 9 and 10) are considerably smaller than some of the specimens of the S. polymorphus, from which I suppose them to have developed. This appeared to me at first a most serious objection, though upon further consideration it does not seem an insurmountable one. The ragged and irregularly constricted ends of some of the specimens (figs. 7 and 8) suggest that part of the body is being lost, as in the case in the development of the strobila in those forms which have a typical bladder-worm stage. Again, while the body region is smaller than that of the larger specimens of the S. polymorphus (fig. 12) the scolex of the young P. triloculatum (figs. 9, 10 and 11) is considerably larger than that of the S. polymorphus. I should also add that fig. 12 represents one of the very largest of the larvae and has been killed under pressure to flatten the body and make it more suitable for a whole mount whereas the specimens of P. triloculatum were killed without pressure and the body has remained cylindrical. The S. polymorphus reaches this size (fig. 12) only in the cystic duct and the smaller specimens present a lesser disparity in size. I am inclined to think that in the case of such large specimens portions of the S. polymorphus body may be moulted off just as in the case of the bladder portion in the cysticercus. One constant feature of the larger specimens of the S. polymorphus has, perhaps, some significance in this connection. It is the occurrence of a denser region which terminates abruptly a little way behind the scolex (fig. 12). In a specimen stained and mounted whole after the carbonate of lime granules, which occupy so much of the parenchyma in the body region, have been dissolved out, one can distinguish this region as having the same denser appearance as the tissue in the body of the young Phoreiobothria (figs. 10 and 12) or the region of proglottid formation in young specimens of C. laciniatum. It is possible that the scolex and this region of the S. polymorphus are the most important in the formation of the adult worm and that part or the whole of the body region may be lost. It seems probable that larvae like the S. polymorphus have been derived from larvae of the cysticercus type and, if this be the case, it would not be surprising to have a part of the body region lost at this point in the development.

SUMMARY

Experimental infections of the sand shark (Carcharias littoralis) with the cestode larva known as the Scolex polymorphus indicate that the larvae used for these experiments developed into the species Phoreiobothrium triloculatum. It seems clear that the common tapeworm (Crossobothrium laciniatum) of this shark cannot come from the Scolex polymorphus, even though this larval type may represent the young of a number of cestodes, a possibility which is referred to in the third section of this paper.

Starving the sharks had no effect upon the cestodes, but by means of treatment with the oil of male fern followed by calomel the great majority of the parasites were eliminated before the sharks were artificially infected. It seems probable that by a little more experimentation a method of treatment could be secured, which, for eliminating these parasites, would be sufficiently effective for all working purposes.

THE SCOLEX POLYMORPHUS

LITERATURE CITED

BRONN, THIERREICH 1894-1900 Cestodes.

- CURTIS, W. C. 1903 Crossobothrium laciniatum and developmental stimuli in the cestoda. Biol. Bull., vol. 5, no. 2, July, 1903.
 1906 The formation of proglottids in Crossobothrium laciniatum. Biol. Bull., vol. 11, no. 4, Sept., 1906.
- LINTON, EDWIN 1886 Notes on the entozoa of marine fishes of New England, with descriptions of several new species. Rept. Commissioner of Fish and Fisheries for 1886. Washington. Published in 1889.

1887 Notes on the entozoa of marine fishes of New England. Part II. Ibid. for 1887. Washington. Published in 1890.

1897a Notes on larval parasites of fishes. Proc. U. S. Natl. Museum, vol. 19, Washington.

1897b Notes on cestode parasites of fishes. Ibid., vol. 20, Washington.
1899 Fish parasites collected at Woods Hole in 1898. Bull. U. S. Fish Commission for 1899. Washington. Published in 1900.

1899 Parasites of fishes of the Woods Hole region. Ibid. for 1899. Washington. Published in 1901.

1904 Parasites of fishes of Beaufort, North Carolina. Ibid. for 1904 Washington. Published in 1905.

- MONTICELLI, F. S. 1888 Contributione allo studio della fauna elminthologico del golfo di Napoli. 1. Richerche sullo Scolex polymorphus. Mitth. zool. Stat. Neapel, Bd. 8, p. 85-152.
- PECK, JAMES I. 1895 The sources of marine food. Bull. U. S. Fish Commission for 1895. Washington. Published in 1896.
- RUDOLPHI, C. A. 1808 Entozoorum sive vermium intestinalium historia naturalis. Vols. 1 and 2. 1808 and 1809.
- VAN BENEDEN, J. P. 1850 Les vers cestoides. Bull. de l'Academ. roy. de Belg. Tome 17, no. 1.
- WAGENER, C. R. 1854 Die Entwicklung der Cestoden nach eigenen Untersuchungen. Nov. Act. d. k. Leop-Carol. Akad. d. Naturf. Bd. 24, suppl., Breslau.
- ZSCHOKKE, F. 1886 Le development du Scolex polymorphus. Arch. d. sc. phys. et. nat., 3 ser., Tome 16, Genève.

PLATE 1

EXPLANATION OF FIGURES

1 Outline of a living specimen of the Scolex polymorphus. The stippled areas just behind the four bothria show the location of the faint red pigment spots seen in some specimens. Magnified about 45 diameters.

2 Specimens of the Scolex polymorphus drawn from the living specimen to show the characteristic mode of attaching with all four suckers to the bottom of a dish in which they are being examined and the manner in which they fasten to one another. Magnified about 45 diameters.

3 and 4 Outlines of the Scolex polymorphus drawn from living specimens to show other characteristic shapes. The area occupied by the large and small vascular trunks of either side and the terminal vesicle are added to fig. 3 as they appear in a stained specimen. The filiform appearance shown in fig. 4 is often seen as the larvae draw themselves over a surface by the characteristic movements of their bothria. Magnified about 45 diameters.

4a From a specimen stained and mounted whole, showing a portion of the body region on a large scale. The cuticle (cu), the larger and smäller excretory trunks (wt) and the conspicuous longitudinal muscle fibres (mf) are shown. The stippling indicates the distribution of nuclei in the parenchyma as it appears in optical section. Along part of the upper margin are shown the minute projections which occur upon the cuticle in the posterior part of the scolex region and for a short distance along the body, finally giving place to the smooth cuticle as shown in the figure. Magnified about 200 diameters.

5 Scolex of a young Phoreiobothrium triloculatum, taken from a sand shark artificially infected with Scolex polymorphus (see shark no. 3 of table 7). This view shows the division between two neighboring bothria along the mid-line of the figure. The characteristic pairs of hooks are shown attached along the line separating the upper and middle loculi of each bothrium. In this figure the subdivision of the posterior margin of the bothrium into three loculi, from which the specific name is derived, is not seen because the contraction of the lower margin brings their surface at right angles to the general surface of the bothrium. The area on the mid-line of the figure toward the anterior end of the scolex, and marked by the closer stippling, appears in some specimens and may represent the 'myzorhynchus' of the Scolex polymorphus. The minute spikes protruding from the neek region of the cuticle are shown in profile only. Magnified about 90 diameters.

6 The same as the last figure. One of the bothria is shown in front view and the three posterior loculi are expanded so as to show clearly. Magnified about 100 diameters.

LIFE HISTORY OF SCOLEX POLYMORPHUS W. C. CURTIS

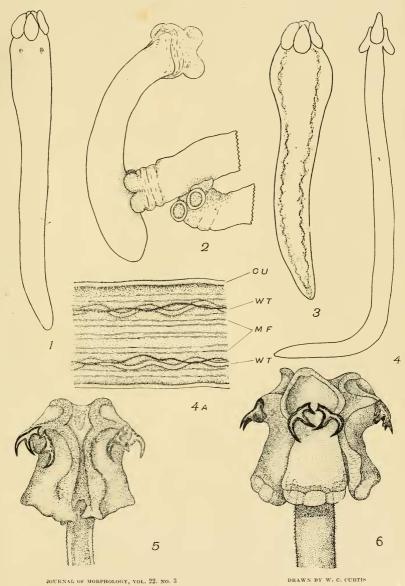


PLATE 2

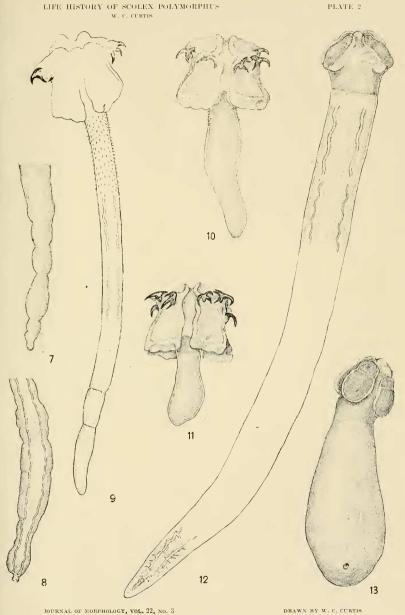
EXPLANATION OF FIGURES

7 and 8 The posterior end of a young specimen of Phoreiobothrium from a shark artificially infected with the Scolex polymorphus. These figures show the formation, either of psuedo-proglottids which are molted, or an irregular beginning of true proglottid formation like that of Crossobothrium laciniatum (Curtis, '06). The figure shows so much irregularity that the process does not seem like true proglottid formation and the posterior end shows a peculiar outline which probably indicates that part of the specimen has been lost. Only the larger pair of the two water trunks is shown. Magnified about 70 diameters.

9 One of the largest specimens of Phoreiobothrium triloculatum which was secured from the artificially infected sharks (see shark no. 8 of table 7). This is one of the few specimens which showed a segmentation of the posterior proglot-tids in Crossobothrium laciniatum. The scolex of the specimen is shown in out-line only. The area of the ninute spikes is shown and back of this the two pairs of water trunks which in such a view are superposed throughout the length of the body, are here shown in successive regions. Magnified about 70 diameters.

10 and 11 Two of the smallest of the specimens of Phoreiobothrium triloculatum obtained from the artificially infected sharks (see shark no. 3 of table 7). The specimens represented in fig. 10 was ragged at the posterior end as though portions had been detached. Magnified about 70 diameters.

12 and 13 Show in more detail the features of the Scolex polymorphus. In fig. 12 the 'myzorhynchus' or proboscis-like structure is shown at the anterior end between the four bothria. The larger and smaller water vascular trunks are shown in successive regions and their convergence toward the posterior end where the vessels become irregular and branched so that they can only be followed as an area of differentiation in the parenchyma. Each bothrium consists of a denser portion divided into three regions or loculi in the older specimens (fig. 12), and in those slightly smaller often showing only the line of division at the anterior end (fig. 13). In fig. 13 the opening of the terminal vesicle of the water tubes is seen in surface view, the posterior end of the specimen being slightly turned toward the observer. Magnified about 70 diameters.



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